Flight Patterns and Mating Behavior in a Zephyrus Hairstreak, *Neozephyrus japonicus* (Lepidoptera: Lycaenidae)

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Abstract: Flight patterns and mating behaviors of a zephyrus hairstreak, *Neozephyrus japonicus*, were investigated in a woodland in Ryugasaki City, Japan, during its adult flight period in late June and July, from 2000 to 2003. This species was most active around dusk, from 17:00 to 18:00 hrs, during which males actively flew around the canopy and edges of the forest. Circling flights performed by two individuals were frequently observed, as were chase flights, sometimes composed of multiple individuals. Circles flown during circling flights averaged 14 cm in diameter and 2.9 rotations/s, thus the velocity of these flights averaged about 130 cm/s. The direction of rotation sometimes changed during circling flights. A third individual occasionally joined a circling flight, which would sometimes disrupt the flight, or rarely, would replace one of the original circlers. Chase flights, sometimes in a zigzag pattern, usually included a female, and sometimes led to the initiation of courtship. Courtship and copulation sometimes occurred just after chase flights. Courtship time was between 30 seconds and one minute, and copulation time varied from 45 minutes to over three hours. Examination of the bursa copulatrix of females of *N. japonicus* from the study site indicated the sporadic occurrence of multiple matings.

Key words: activity time, circling flight, chase flight, mating, Lycaenidae, spermatophore

Introduction

Butterflies in the tribe Theclini, commonly called "zephyrus hairstreaks" in Japan, are biologically interesting for a variety of reasons. This relatively small group shows great variation in adult and larval morphologies, life histories, physiology, behavior and ecology (Saigusa 1988). In Japan, this group includes 25 species in 13 genera such as *Chrysozephyrus*, *Neozephyrus* and *Favonius*, whose phylogenetic relationships have been studied, using morphological (Shirôzu & Yamamoto 1956) and molecular data (Saigusa & Odagiri 2000).

An intriguing aspect of the Theclini in Japan is variation in wing colors; 13 species show sexual dimorphism, 11 species are nearly or perfectly monomorphic, and 1 species is in an intermediate situation. Some species of *Chrysozephyrus*, *Neozephyrus* and *Favonius* show the most conspicuous color differences between sexes among butterflies occurring in Japan. These color variations may be related to the behavior and ecology of the various species. Males of some species are territorial, and mate-locate by guarding perches, whereas others mate-locate through patrolling. Adult activity times vary among the different species; some are active early in the morning, some during midday, and others are most active at dusk (Fukuda et al. 1984). However, published information on the behavior and ecology of the zephyrus hairstreaks is incomplete, and systematic studies on the ecology of these hairstreaks have not been previously conducted. This is partly because adults are largely arboreal, and thus, makedifficult subjects for behavioral or ecological studies.

Previously, the senior author observed mating behaviors of one of the sexually dimorphic zephyrus hairstreaks, *Neozephyrus japonicus* (Murray, 1845),

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males of which have metallic green scales on the dorsal surface of the wings, while females have mostly brown or black wings above. Two attempts at courtship, and one copulation event were witnessed, among 22 individuals released in a large cage (Imafuku et al. 2000). Subsequently, the junior authors observed copulation events among wild pairs of *N. japonicus*. Their results were reported at the meetings of the Lepidopterological Society of Japan from 2000 to 2002. Since then, we have conducted a systematic investigation of mating and related behaviors of a wild population of *N. japonicus*. Herein we present the results of those studies, including details of mating behavior from the initiation of courtship to final copulation, along with information on diurnal activity, circling and chase flights, and experimental results on male responses to female models.

Materials and Methods

Study area

This study on the behavior of *Neozephyrus japonicus* was conducted in a small wooded area in Ryugasaki City, Ibaragi Pref., Japan (35°55'N 140°10'E), during the butterfly's adult flight season, from the end of June to July, 2000 to 2003. The wooded area was divided by a narrow lane into two sections; one composed of tall (10-15 m) alder trees, *Alnus japonica* Steudel, and the other composed of willow trees (4-6 m), including *Salix subfragilis* Andersson and *S. chaenomeloides* Kimura (fig. 1). *Alnus japonica* is a local foodplant for larvae of *Neozephyrus japonicus*. The study site was surrounded by grasses such as the reed *Phragmites communis* Trinius, the goldenrod *Solidago altissima* L., and also by cultivated fields.

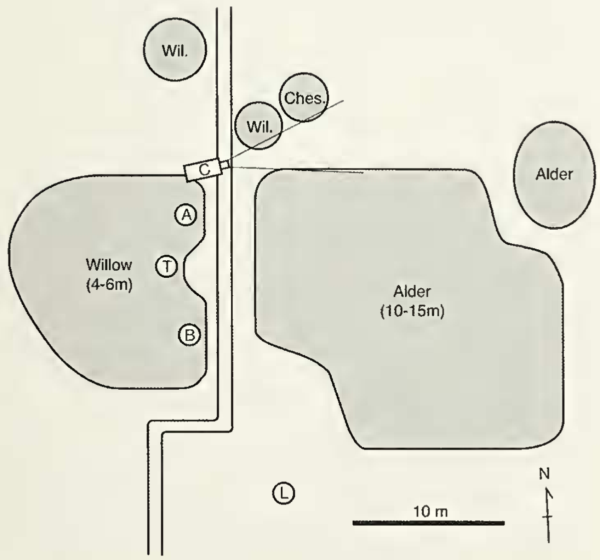

Fig. 1. Study site in Ryugasaki City, Ibaragi Pref., Japan. Patches of willow and alder trees were separated by a path. A thermometer (T) and an illuminator (L) were placed as indicated. A digital video camera (C) was installed for observations of a fixed area, north of the alder grove. A and B indicate sites at which individuals of *N. japonicus* were marked (see Results). Wil. = willow; Ches. = chestnut.

Observation of diurnal activity

The number of butterflies observed in flight was recorded every 15 to 60 minutes, from dawn to dusk, by slowly walking along the lane. The air temperature was recorded every 5 minutes with a temperature data logger (Gemini Data Logger, temperature) settled in the willow grove (T in fig. 1). The light intensity was recorded by an illuminator situated in open space (shown with L in fig. 1), and data were stored every 5 minutes in a second data logger (Gemini Data Logger, voltage). These counts were conducted from June 30 to July 2, 2002.

Observation of flight activity using a video camera

These surveys were conducted on 4 days between July 2 and 7, 2002. During the peak time of adult activity, near dusk, many butterflies were observed flying over the canopy and edges of trees, occasionally performing chase flights and circling flights (or the spiral flight described by Davies 1978). To record a detailed temporal sequence of changes in these activities, a digital video camera (Sony, DCR-TRV20) was set at a fixed point (C in fig. 1) to record flying butterflies. The camera remained stationary, and recorded individuals that appeared on the north side of the alder woods. Numbers of butterflies, of circling flights and of chase flights appearing every 10 minutes were recorded from 16:30 to 19:00 hrs. Numbers of butterflies were estimated by treating each individual appearing on the screen, until the time it disappeared from view, as separate individuals. The air temperature and light intensity were recorded with a thermometer and illuminator (Mother Tool, LX-100).

Detailed observations and experiments

In order to document detailed patterns of circling and chase flights, butterflies were recorded with a hand-held digital video camera. Recorded images were then incorporated into a personal computer using "iMovie, 2.1.1" (Microsoft), and flight paths were plotted using "NIH images, 1.62" (courtesy of the National Institute of Health, USA). For drawings in figs. 5 and 6, and in measurements of flight velocity, a reduced scale was calculated by comparing the image size of a butterfly on the computer screen to the average natural size of butterflies collected at the study site. Two arbitrarily determined reference points were also plotted to compensate for changes in images caused by zooming and movement of the camera during recordings.

As chase flights were inferred to occur on participation of a female, two model experiments were performed. In the first experiment ("female model," July 4, 2001), a female hairstreak was allowed to fly, but was tied to the tip of a 3.3 m fiberglass rod with 60 cm of cotton string (#50) secured to her thorax, between the fore-and hindwings. In the second experiment ("female wing model," July 7, 2001), female wings were pasted on both sides of a plastic figure (made from a plastic plate), shaped to mimic a female hairstreak holding its wings open, which was secured to a rod and rotated with a small motor. In each experiment, models were situated in areas where male hairstreaks were active.

In order to determine the sexes of butterflies involved in chase flights, capture with an insect net was attempted. For observations of mating behaviors, binoculars and a video camera were used, and detailed verbal descriptions of various processes were recorded on the latter.

Results

Diurnal activity

Adults of *Neozephyrus japonicus* were most active from 17:00 to 18:00 hrs., just before dusk (fig. 2). This period of peak activity was essentially the same on clear days (e.g., June 30 and July 2, with the highest air temperature over 28°C and the maximum light intensity exceeding 60,000 lux) as it was on cloudy days (e.g., July 1, with temperatures lower than 25.5°C through the daytime and the maximum light intensity lower than 20,000 lux). On clear days, some adult activity was observed in the morning. Shortly before the period of peak adult activity, around 16:00 hrs., females were frequently observed on grasses around the woods, sometimes basking with open wings. As time elapsed, they moved to higher sites in the trees. Around 16:30 hrs., males started to fly over the sides and canopy of the alder and willow groves, andoccasional circling flights by two males were performed. As it became darker, chase flights occurred, in which some butterflies appeared to be rapidly chasing other individuals. With increasing darkness, numbers of flying hairstreaks decreased, and no butterflies were observed by 19:30 hrs.

Evening flight activity

Observations recorded with the fixed video camera during the evening period of peak activity are shown in fig. 3. Flying butterflies first appeared at 16:55 hrs., when the light intensity was 13,000 lux, and numbers of flying butterflies gradually increased with a peak around 18:15 hrs. (fig. 3b). The average time of peak adult activity was calculated to be 18:07 hrs. The lightintensity at this time was about 4,000 lux. After this time, the number of flying butterflies gradually decreased.

Circling flights started to occur as number of flying butterflies increased, and continued until flight activity ended (fig. 3a). The frequency of chase flights

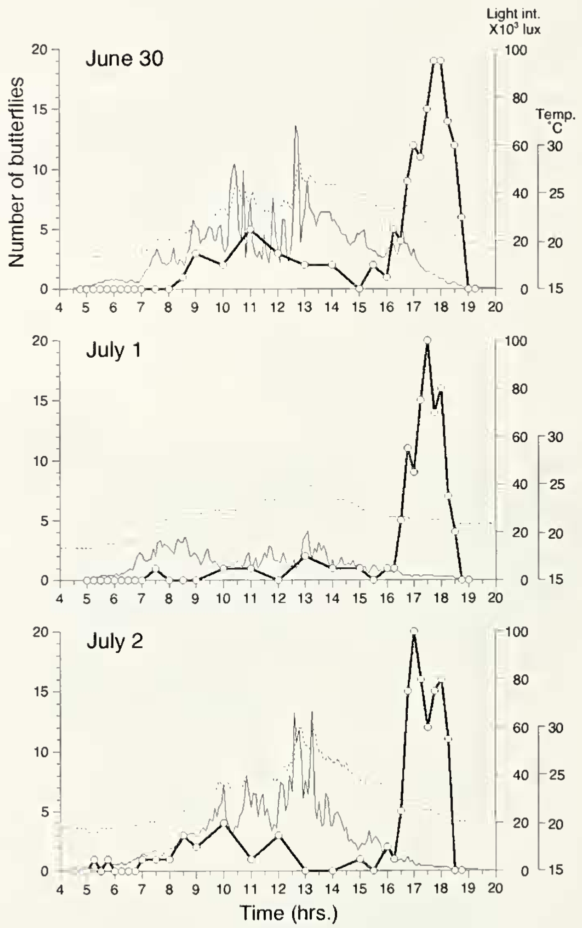

Fig. 2. Changes in the number of flying individuals of *N. japonicus* (thick line) on three days in 2002. Thin and dotted lines indicate light intensity and temperature, respectively. Two days (June 30 and July 2) were sunny, while July 1 was cloudy.

Table 1. Diameter and rotation speed of circling flights in *Neozephyrus japonicus*.

Sample	Sampling time (s)	Diameter (cm)	Rotation speed (rounds/s)
#1	1.30	11	3.8
#2	1.50	12	2.9
#3	2.77	16	2.6
#4	2.93	15	2.4
#5	3.73	19	2.6
#6	2.07	12	3.2
#7	2.63	11	3.1
#8	2.63	20	2.1
#9	3.13	12	3.3
#10	1.97	15	3.1
Average	2.47	14	2.9
Range	1.30-3.73	11-20	2.1-3.8

was greater in the later half of the evening activity period. The greatest average number of circling flights occurred at about 18:05 hrs., while the greatest number of chase flights occurred slightly later, at about 18:20 hrs.

When males were active in circling flights, capturing attempts were made for butterflies straying around a canopy or sub-canopy level, with a result that 4 out of 5 captured individuals were females. Flight behavior of females appeared to be somewhat different than that of males, in that they flew slightly slower, and at a lower altitude.

Circling flights

Circling flights involved two male butterflies, each flying rapidly in a small circle. Most circling flights were completed in a few seconds, whereas some lasted longer. Durations of 46 circling flights observed from July 12 to 17, 2002, are shown in fig. 4. Most circling flights (72 %) were completed within 30 s. The longest circling flight lasted 6 min 18 s. The diameter of the circle varied from 11 cm to 20 cm, with an average of 14 cm (Table 1). Butterflies engaged in a circling flight rotated 2.1 to 3.8 times per second, 2.9 times on average. Thus, their flight velocity in circling flights was calculated to be about 130 cm/s.

A trace of a typical circling flight is shown in fig. 5b. Circling flights were frequently initiated when males happened upon each other, either through random movements (fig. 5a), or through a chase. Rotation direction was not always fixed, and as shown in fig. 5c, sometimes changed. In some cases, a third individual joined into ongoing circling flights. Out of 46 circling flights observed, 14 were invaded by a third individual. Among these, six were continued by the original circlers with the third butterfly flying away (fig. 5e), six were broken up, and two were continued by the original and the newly arrived third individual (fig. 5f). At the end of circling flights, one of the circlers flew away sometimes, chased by the other (fig. 5d).

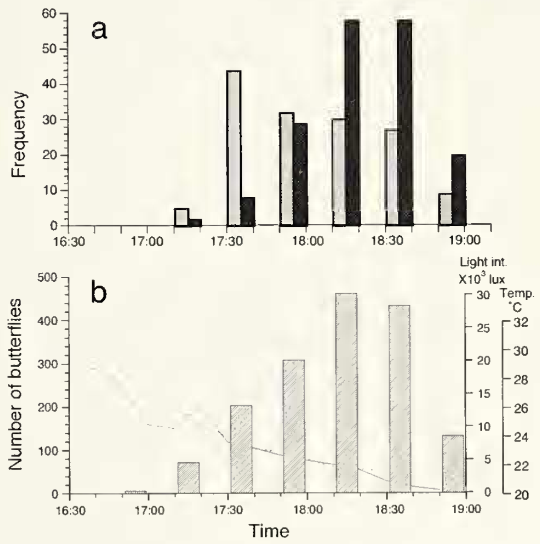

Fig. 3. a. Temporal distribution of circling flights (gray bar) and chase flights (solid bar) during the evening activity period of *N. japonicus* at the study site. b. Temporal distribution of flying butterflies at the study site. Light intensity and temperature are shown with solid and dotted lines, respectively.

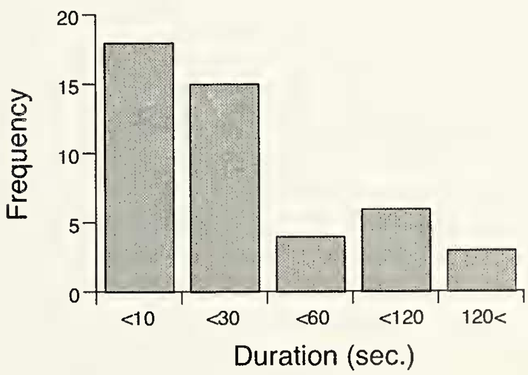

Fig. 4. Frequency of circling flights in *N. japonicus*, plotted against their duration.

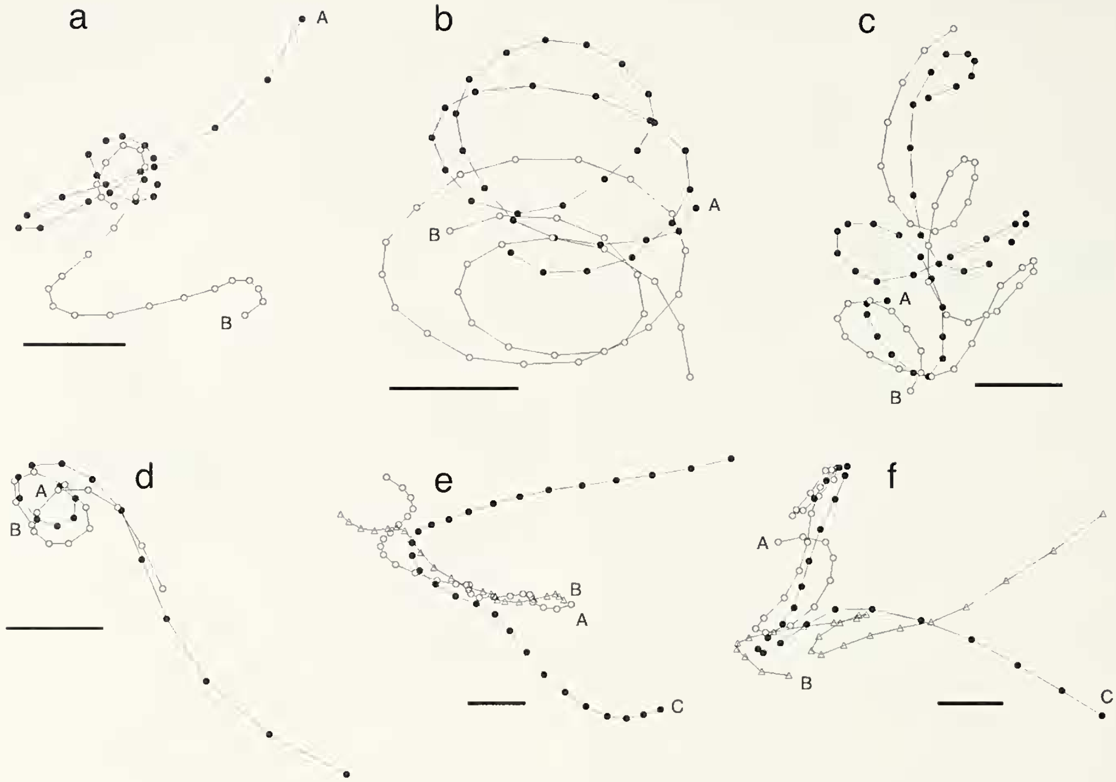

Fig. 5. Traces of flight patterns related to circling flights of *N. japonicus*. In each figure, alphabetical letters (upper cases) indicate individual butterflies and their positions in the first frame of the figure. Each point on the trace line represents the position of the butterfly in successive frames, thus, every 1/30 s. A scale bar below each figure indicates 10 cm. a. Initiation of a circling flight (17:12:55, July 1, 2002). b. Typical circling (18:09:44, July 1, 2002). c. Change of rotation direction; the initial right rotation for the butterfly (left rotation for the observer below) changes to a left rotation (17:48:11, July 1, 2002). d. End of circling, resulting in a chase of one butterfly (A) by the other (B) (18:14:52, July 1, 2002). e. Approach and subsequent retreat of a third butterfly (C) to a circling flight (17:34:21, July 1, 2002). f. Replacement of circlers. One of the initial circlers (A) continues to circle with the invader (C), while the other circler (B) retreats (18:00:37, July 12, 2002).

Residency

Circling flights or spiral flights are usually shown by territorial species (see Discussion). Males of *Neozephyrus japonicus* in the study area did not show clear territorial behavior, but some males repeatedly flew around a specific parts of the canopy. Therefore, residency was examined for our population. Two butterflies at points A and B on fig. 1 were captured and marked with a black felt-tip pen on the undersides of the wings at about 18:00 hrs on June 29, 2002. The butterfly marked at point A was recaptured at the same site and at similar times the following 3 days, until observations at the site were terminated. The butterfly marked at point B was recorded from the same site the following 2 days, but not on the last day of the study. Thus, butterflies in the study field exhibited a certain degree of residency.

Chase flight

Chase flights were occasionally initiated immediately after circling flights, and sometimes involved multiple individuals (fig. 6d). Some chase flights were very persistent, covering a larger distanceimmediately after circling flights. Rarely, zigzag flights involving two individuals were observed. A trace of a zigzag flight is shown in fig. 6b, where one butterfly (A) approaches another (F), and proceeds to follow it closely. The chasing butterfly (A) showed a similar turning pattern to that of the butterfly being chased (F), with a delay of 2 to 3 frames (67 to 100 msec).

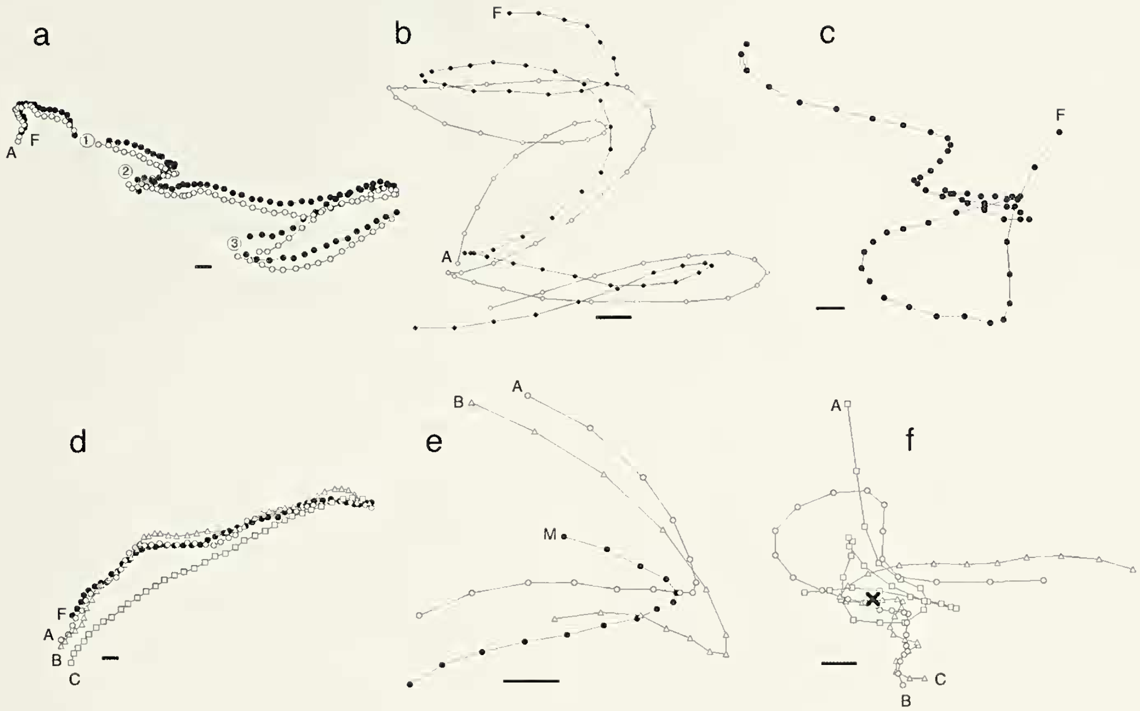

Fig. 6. Traces of flight patterns related to chase flights of *N. japonicus*. Presentations are the same as in Fig. 5, unless otherwise noted. a. A persistent chase of a presumed female (F) by a male (A). Traces were interrupted because of tree branches; 12, 31 and 24 frames were lacked at circles 1, 2 and 3, respectively. This chase continues at least 5.8 s (17:51:26, July 2, 2002). b. A zigzag flight. A presumed female (F) is chased by a male (A) which approaches from below (17:02:56, July 2, 2002). c. Flight path of the presumed female prior to chase by a male, showing a "swinging" flight. The final point of this figure continues to the start point of figure b (17:02:54, July 2, 2002). d. A group chase. A presumed female (F) is always at the lead. "The male "C" appears in the figure after at the 12th frame (17:22:07, July 2, 2002). e. Chase flight by two males (A & B) to the tied female model (M) (18:28:29, July 4, 2001). f. Simultaneous approach of a solitary male (A) and circling males (B & C) to the female wing model (shown with a cross near the center) rotated by a motor (17:58:03, July 7, 2001).

Zigzag flights observed at the study site are thought to involve the chasing of a female by a male (see Discussion). Prior to the zigzag flight shown in fig. 6b, the presumed female (F) descended from the alder canopy into an open space, where she flew in a swinging flight (fig. 6c).

Occasionally, a hairstreak was observed to approach a circling flight involving two males, which resulted in the chasing of the third individual by the two males that had been circling. In cases such as this, the approaching individual may have been a male (as seen in figs. 5e and 5f), but in several cases it was thought to be a female, because the resulting chase by males was very persistent.

The model experiments sought to test the idea that chase flights are frequently composed of a male (chasing) and female (leading) hairstreak, and the reactions of males upon identifying a potential female mate. Multiple males were attracted to the "female model" tied with thread, and closely followed her flight when she turned sharply (fig. 6e). In fig. 6e, the chasing male followed the abrupt turn of the tied female with a delay of about 2 frames (67 msec). When the "female wing model" rotated by a motor was revealed at the study site, one or more males were frequently attracted (fig. 6f). It should be noted that males engaged in circling flights were sometimes attracted by both of the models.

Finally, the capture of butterflies engaged in chase flights was attempted, using an insect net. Among each of the three successful captures, one female and one male was involved.

Table 2. Copulation statistics for *Neozephyrus japonicus*

Case	Date	Time	Temp.	Duration	Site (from the ground)
#1	10-7-'00	18:46	24.5°C	-	on an alder leaf at 3.8 m
#2	12-7-'01	18:20	27.5°C	ca. 3:20	on a goldenrod leaf at 1.2 m
#3	15-7-'01	18:20	28.5°C	3:18-21	on a goldenrod leaf at 0.9 m
#4	12-7-'02	18:20	25.5°C	-	on an alder leaf at 4.0 m
#5	15-7-'02	18:13	28.5°C	3:07*	on a willow leaf at 1.8 m
#6	17-7-'03	17:13	21.6°C	3:43-4:27	on an alder leaf in 4-5 m
#7	17-7-'03	17:48	21.6°C	5:12-6:08	on an alder leaf in 4-5 m
#8	18-7-'03	17:22	20.9°C	3:40-4:38	on an alder leaf in 4.5 m

*Pairs were carefully brought to a room (30.0°C) and continuously observed.

Courtship and copulation

During the study period from 2000 to 2003, eight instances of copulation were witnessed (Table 2). Copulation usually occurred on leaves, between 3 to 5 m above ground level. On July 10, 2000, at 18:46 hrs, a chase flight involving four butterflies was broken up when a male and a female split away from the group, and landed on an alder leaf 3.8 m above ground level. Subsequently, the male situated himself at a right angle to the female. About 30 seconds after landing, the male walked toward the female and aligned himself next to the female, in a parallel position, so that they were both facing the same direction. Five to six seconds later, the male curved the tip of his abdomen toward the female's genitalia, and after another five to six seconds, succeeded in connecting with the female, to assume a V-shaped body position. At 18:47, the male straightened his figure, and the butterflies faced opposite directions in a normal end-to-end copulation posture. Then, they remained stationary for several hours. At 4:25 hrs the following morning, the pair was found separated. Anatomical examination of the female revealed one spermatophore in the bursa copulatrix.

On July 15, 2001, a copulation event was witnessed after a pair of hairstreaks landed on a goldenrod leaf 0.9 m above ground level, permitting close observations. Upon landing of the female, the male barely clung to the leaf on which the female normally perched. After the male climbed up the leaf, it approached the female from behind at an angle of 60°. Once the male had oriented himself to be side by side with the female, in a parallel position, he retreated slightly, sharply curving the posterior part of his abdomen to contact her genitalia. About 30 seconds elapsed between the time when the pair landed on the goldenrod leaf and the time they assumed a normal end-to-end copulation posture.

Pairs of hairstreaks landing together after a chase flight sometimes did not couple. In three such cases (17:45 and 17:55 on July 11, and 18:00 on July 12, 2000) copulation attempts ended in failure when the female flew away, even though in one case the male attempted copulation. In most of the copulation attempts observed, males did not open or flutter their wings. However, on July 12, 2002, one male slightly but rapidly and repeatedly fluttered his wings, while situated next to the female, prior to successful copulation. As shown in Table 2, copulation times observed for *Neozephyrus* varied from about 45 minutes to 3 hours and 20 minutes. To check for multiple matings, the bursa copulatrix of 8 females was examined. Five of these females possessed one spermatophore, one female had two, and two females had three.

Discussion

Activity time

Different species of zephyrus hairstreaks are most active at different times during the day. Previously, *Neozephyrus japonicus* has been described as being most active around dusk (Fukuda et al. 1984), but no detailed observations were presented. Herein, we have documented that the peak activity period of wild *N. japonicus* adults is between 17:00 hrs and 18:00 hrs.These results agree with those of an earlier study on a captive population of *N. japonicus,* where adults remained inactive until 16:00 hrs, and were most active after 17:00 hrs (Imafuku et al. 2000).

Peak periods of activity for some other zephyrus hairstreaks have been determined using quantitative data. As shown by Kôda (1982) for *Chrysozephyrus* *brillantinus* (Staudinger, 1887) and by Takeuchi & Imafuku (2005) for *Favonius taxila* (Bremer, 1864), some species are most active during the morning, from 7:00 to 11:00 hrs. Hirowatari and Ishii (2001) showed that *Favonius cognatus* (Staudinger, 1892) is most active during midday, from 10:00 to 14:00 hrs. According to Kôda (1982), adults of *Chrysozephyrus smaragdinus* (Bremer, 1864) and *Favonius orientalis* (Murray, 1875) are most active from 8:00 or 9:00 to 16:00 hrs, with suppression of activity during periods of great light intensity. A bimodal pattern with activity peaks in the morning and evening is known for *Artopoetes pryeri* (Murray, 1873) (Kôda 1982), Antigius attilia (Bremer, 1861) (Kôda 1982; Hirowatari & Ishii 2001) and *Favonius saphirinus* (Staudinger, 1887) (Hirowatari & Ishii 2001). As shown by Akiyama et al. (1969) and Hirowatari & Ishii (2001), *Japonica saepestriata* (Hewitson, 1865) is most active during the evening hours. Thus, times of peak adult activity are very different among different species of zephyrus hairstreaks. Species-specific activity times might be explainable in terms of predation pressures and intraspecific mating behaviors.

The evening crepuscular activity of *Neozephyrus japonicus* may be related to predator evasion. Birds are known to be one of the most important predators of butterflies, and their activities usually decline at dusk. Swallows, however, were sometimes witnessed to attack circling males of *N. japonicus* during our observations, and some butterfly specimens collected during the course of this study had "beak marks" (Johki 1985) on their wings. Thus, it seems possible that the time of peak activity for adult *N. japonicus* is situated between the time in the evening when most local bird species become inactive, and when it becomes too dark for hairstreaks to see.

Circling flights

In *N. japonicus*, the diameter of circling flights averaged about 14 cm (Table 1). Apparently, the diameter of circles flown by other species of zephyrus hairstreaks has not been measured. However, Fujii (1982) illustrated flights of *Chrysozephyrus smaragdinus*, *Favonius taxila*, *Iratsume orsedice* (Butler, 1881), and (Hewitson, 1865) in "small circles." In contrast, the diameter of circles flown by another lycaenid, *Holochila helenita* (Semper, 1879), extends up to 1-2 meters (Sibatani 1998). Among nymphalid butterflies, Davies (1978) depicted two individuals of *Pararge aegeria* (Linnaeus, 1758) spiraling in small circles, and Sibatani (1998) observed a co-rotating flight of 20-50 cm in diameter for *Mycalesis gotama* Moore, 1857. Sibatani (1998) also observed *Hypolimnas bolina* (Linnaeus, 1758) flying in a circle with a diameter of 50 cm to 1 meter. Bitzer & Shaw (1979) figured a trace from the flight of a red admiral, *Vanessa atalanta* (L., 1758), flying in an ascending helical path, as large as 9 meters in diameter.

Circling individuals of *N. japonicus* occasionally changed the direction of the spiral, as shown in fig. 5c. Such changes were also observed in circling flights of M. gotama (Sibatani 1998). However, two interacting individuals of *V. atalanta* reportedly circled "most often in a counter clockwise direction as seen from below" (Bitzer & Shaw 1979).

As for circling or spiral flights, some functions have been proposed. A contest for occupation of territories by males of territorial species has been widely accepted (Baker 1972; Davies 1978; Bitzer & Shaw 1979; Wickmann & Wiklund 1983; Takeuchi & Imafuku (2005). *Neozephyrus japonicus* was described as a territorial species by Fukuda et al. (1984). The two individuals of *N. japonicus* that were marked during our study and observed for several days persisted in guarding the same perching sites, day after day.

As noted by Sibatini (1989), circling flights are also known for non-territorial butterfly species such as *Holochila helenita*, *Eurema blanda* (Boisduval, 1836) and *Neptis sappho* (Pallas, 1771). This suggests that the behavior is not always related to the defense of a territory, but that it may serve to aid in recognition of potential mates (Scott 1974; Suzuki 1976).

A further possible explanation for circling flights among males of *N. japonicus* could be to attract females. Such a scenario may parallel displays by two males toward a female as seen in manakin birds (Snow 1963; Grzimek et al.1968), where ornamented males show a specific synchronous dance in front of a female.This idea is discussed in further detail below.

Chase flights

Chase flights between two individuals sometimes attracted the attention of other hairstreaks, and small groups were occasionally involved in chases. Capture of hairstreaks engaged in chase flights revealed that such flights included at least one female. Chase flights were often terminated when two individuals break out of the chase, and land near each other. This often led to subsequent courtship or copulation. Thus, chase flights are thought to represent the pursuit of a female by males, and may be one of the steps in courtship.

Zigzag flights observed in the present study (fig. 6b) seem to be a type of chase flight, where a female is being chased by a male. A similar flight pattern was observed in another zephyrus hairstreak, *Chrysozephyrus smaragdinus* (Imafuku pers. obs.). Males of

C. smaragdinus have brilliant green wings above, and are most active during midday, from 10:00 to 16:00 hrs. Therefore, we could easily determine that zigzag flights were composed of a male and a female. It seems possible that females are exerting some selective choice on males, perhaps as judged through their maneuverability, during zigzag flights.

Courtship and copulation

Courtship and copulation events between pairs of N. japonicus were witnessed throughout the peak activity period of adults, around dusk, and usually occurred on vegetation between three and five meters above ground level. The timing and placement of these events may protect coupled pairs of *N. japonicus* avoid diurnal predators, and may help them avoid terrestrial predators, such as centipedes and carabid beetles, through periods of relative inactivity during the night.

Duration of copulation between pairs of *N. japonicus* ranged from 3 to 6 hours (Table 2). This does not largely differ from times observed among individuals of *N. japonicus* in captivity, between 2.5 and 3.5 hours (Imafuku et al. 2000). Scott (1973) summarized copulation times for various butterfly species. Extremes included 10 minutes for *Papilio xuthulus*, two days for some *Parnassius* and *Pieris* species, and among lycaenids, two to eight hours for *Callophyrus augustinus* (Westwood, 1852) and 1 hour or more for *Nordmannia ilicis* (Esper, 1779). According to Wiklund (2003), copulation times varied from 10 min in *Coenonympha pamphilus* (Linnaeus, 1758) to a week in *Gonepteryx rhamni* (Linnaeus, 1758).

Multiple matings were confirmed among females of *N. japonicus*. This phenomenon is widespread among butterfly species. Scott (1973) examined females of various butterfly species and found that about 95 % of those species sometimes engaged in multiple matings. Suzuki (1988) studied the number of spermatophores in females of 29 butterfly species, and found that all of them possessed two or more spermatophores, except *Lycaena phlaeas* (Linnaeus, 1761) with had only one. The maximum number of spermatophores found in a single female butterfly was 15 in a female of *Danaus gilippus* (Cramer, 1775). Seventeen papilionid species studied by Matsumoto & Suzuki (1995) included female individuals that had mated more than once, and some females of *Papilio helenus* Linnaeus, 1758 and *P. bianor* Cramer, 1777 had mated 6 times. Thus, the phenomenon of multiple matings seems to be general among butterflies. The function of multiple matings for females is thought to include the production of heterogeneous offspring (ref. Suzuki 1988), or the acquisition of nutrients by females from spermatophores contents (Boggs & Gilbert 1979).

The function of male coloration deserves further discussion. Since the fittest males in various animal populations are often those who successfully compete for mates (Krebs & Davies 1981), male coloration in sexually dimorphic species may serve to attract or court females. As early as 1874, Darwin (p. 505) proposed this hypothesis when he noted that "when we see many males pursuing the same female, we can hardly believe that the pairing is left to blind chance—that the female exerts no choice, and is not influenced by the gorgeous colours or other ornaments with which the male is decorated." Scott (1973: 101) subsequently noted that "this places selective pressure on males to develop sexual characteristics to make the unreceptive females receptive, ... This may explain why males have brighter colors..." Rutowski (1985) showed that males of *Colias eurytheme* Boisduval, 1852 with strong UV reflectance patterns were more readily accepted as mates by females than were males with weak or no UV reflectance. However, Silberglied (1984) could not confirm this for the nymphalid *Anartia amathea* (Linnaeus , 1758), in which males preferred colorful females but females apparently exhibited no choice between colorful and colorless males. If male coloration serves to attract or court females, it seems that males should actively display their wings during courtship. During courtship between pairs of the sexually dimorphic lycaenid *Pseudozizeeria maha* (Kollar, 1844), the male's wings are held wide open, as seen in photos by Wago et al. (1976) and Wago (1978), or may be violently fluttered, demonstrating the conspicuous blue upperside coloration (pers. obs.). However, such behavior was not observed among courting males of *N. japonicus*, although slight fluttering of wings was seen on one occasion. In our study, presumed females of *N. japonicus* were occasionally observed to approach a pair of circling males, resulting in the formation of a chase flight. In such cases, the female may have been attracted by male coloration, but at the moment, no evidence to support this idea has been presented. Further studies on the function of male coloration and of circling flights in *N. japonicus* are needed.

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